Non-*Ribes* Alternate Hosts of White Pine Blister Rust: What this Discovery Means for Whitebark Pine

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From early to present-day outbreaks, white pine blister rust caused by the fungus *Cronartium ribicola,* in combination with mountain pine beetle outbreaks and fire exclusion has caused ecosystem-wide effects for all five-needled pines (McDonald and Hoff 2001). To be successful, efforts to restore whitebark pine will require sound management decisions that incorporate an understanding of many interacting factors, including the biology and life cycle of the fungus, whether it may adapt and change its behavior when exposed to different environments and hosts, and mechanisms and predicted frequencies of resistance in current and regenerating stands and populations of its hosts. Despite the long history of white pine blister rust on whitebark pine, significant gaps in our knowledge of the pathogen, the disease, and resistance are increasingly apparent. Our recent discovery of non-*Ribes* alternate hosts for the white pine blister rust fungus is an illustration of this point.

What is an alternate host? This term refers to one of the two quite different hosts needed by many rust fungi to complete their complex life cycle. For *C. ribicola* in North America, whitebark pine and other five-needled pines are primary hosts. Infections on these hosts cause perennial cankers that produce two of the five stages of the life cycle (pycnial and aecial stages). Aeciospores, which form within blister-like structures on five-needled pines, cause annual infections on dicotyledonous plants. These latter hosts are referred to as alternate hosts. Alternate hosts produce urediniospores that cause cycles of infection on alternate hosts, and teliospores. Basidiospores produced by teliospores cause infections on five-needled pines (McDonald and Hoff 2001).

Until 2004, species of *Ribes* (currants and gooseberries) were the only known natural alternate hosts of *C. ribicola* in North America. That assumption shaped most efforts to control white pine blister rust and predict its spread and intensification. Those efforts included a 50-year program of *Ribes* eradication (Maloy 1997) estimated to cost over a billion US dollars in current valuation (McDonald et al. 2006).

In August of 2004, at a site about 1800 m in elevation west Bonners Ferry, Idaho, suspicious rust infections were found on several non-*Ribes* plant species. The plant species in question are all hemiparasitic on other plants and are in two different genera (*Castilleja* and *Pedicularis*) of the family Orobanchaceae (previously included in the Scrophulariaceae; see Olmstead et al. 2001). The infected species were very abundant on the site, which had been burned in a large fire 38 years before; wind-disseminated seed in these genera (Allard 2001) may have favored their dense establishment.

Teliospores observed on plants in the Orobanchaceae (Figure 1) resembled *C. ribicola* in morphology, but they were also indistinguishable from *C. coleosporioides*, a native fungus that causes a different rust disease that affects lodgepole pine (*P. contorta*), *Castilleja*, and *Pedicularis.* Both whitebark pine and western white pine (*P. monticola*) were present and heavily infected with white pine blister rust at this site; lodgepole pine was found at slightly lower elevations.

DNA-based methods provided a practical approach for identifying infections on these plants (McDonald et al. 2006). From repeated tests, two non-*Ribes* plant species were newly identified as natural hosts of *C. ribicola* in North America: sickletop lousewort (*Pedicularis racemosa*) and a species of Indian paintbrush (*Castilleja miniata*).

The ability of both *P. racemosa* and *C. miniata* plants to act as alternate hosts of *C. ribicola* was further proven by successfully infecting plants of both species in the laboratory using rust aeciospores from whitebark pines. Urediniospores from the artificially inoculated *P. racemosa* plants infected *Ribes*, showing that collections from whitebark pine at the discovery site were not specialized to just one alternate host genus (McDonald et al. 2006). Telia were then used to infect western white pine (*P. monticola*) seedlings, which produced pycnia to complete the life cycle. Lack of host specialization was also supported by studies that used molecular markers to measure differences in *C. ribicola* among primary (whitebark pine and western white pine) and alternate hosts (*Ribes* and *Pedicularis*) at the discovery site; genetic differences were minimal among rust collections from the different hosts (Richardson 2006).

More recently, in 2005, we demonstrated that aeciospores from western white pine at a second location in northern Idaho (ca 200 km south of the first site) would cause infections under natural field conditions when dusted onto local plants of *P. racemosa*. Also, spores from this site infected a second paintbrush species, *C. rhexifolia,* under laboratory conditions (Zambino et al. In Press). Infections of *P. racemosa* at an upper elevation site in northern California were also proven to be *C. ribicola* (D. Vogler, USDA-FS PSWS, pers. comm.).

The finding of multiple sites where *C. ribicola* infects non-*Ribes* hosts shows that utilization of these hosts is not just a concern for northern Idaho. Additional studies will be needed to determine whether different populations of the rust fungus differ in their capacity to infect non-*Ribes* alternate hosts, and whether local populations of alternate hosts differ in their susceptibility to blister rust. Such studies will be important for answering the critical questions of 1) whether this newly discovered infection of non-*Ribes* alternate hosts represents a new adaptation in *C. ribicola* that may arise in different locations, or a widespread and inherent trait that may have been previously overlooked, and 2) whether non-*Ribes* alternate hosts are more important for causing pine infections at some locations than at others.

The ability to adjust to new environments is a common, if not critical trait of invasive species, including pathogens (McDonald et al. 2005). However, some evidence indicates that infection of *Pedicularis* spp. and *Castilleja* spp. could represent a natural ability of the rust that pre-dates its introduction to the western United States. A related species, *P. resupinata*, is known to be an alternate host for some strains of blister rust in Asia, which is a putative origin for the blister rust fungus in Europe and North America (reviewed in McDonald et al. 2005).

Regardless of the source of this ability, the utilization of non-*Ribes* alternate hosts by *C. ribicola* may be useful for explaining high rates of infection at some sites on which *Ribes* are rare or lacking. We speculate that non-*Ribes* alternate hosts may be particularly important for causing blister rust infection within whitebark pine ecosystems, as *Pedicularis* and *Castilleja* species can be very abundant at high elevations. Also, as-yet undetected hosts species could also be involved in spreading infection to whitebark pines. However, surveys will be needed to determine the occurrence and prevalence of blister rust on non-*Ribes* species. These efforts could be aided by readers of Nutcracker Notes and others who frequent high-elevation pine stands. Rust-infected samples of *Pedicularis* and *Castilleja* species that are collected along with GPS coordinates and sufficient floral or seed capsule structures to identify the plants to species will expand our knowledge of where such infections occur. They may even allow a short "first report" note to be published that documents the occurrence of *C. ribicola* on a host not previously listed for a state. To contribute non-*Ribes* samples for DNA-based verification of *C. ribicola* infections, please phone or e-mail Paul Zambino (208-883-2334; pzambino@fs.fed.us) or Bryce Richardson (208-883-2311; brichardson02@fs.fed.us).

The roles of the newly discovered hosts in the infection cycle in pine stands represent a primary research issue that will be important to management. Roles could range from simply increasing leaf tissue for colonization and production of pine-infecting spore stages, to complex and synergistic interactions among different hosts, as has been suggested for some combinations of *Ribes* species (Van Arsdel et al. In Press). As an example, observations at the first site in 2004 and 2005 appeared to show that *P. racemosa* was producing fresh leaves that could be infected by rust even late in the season, but teliospores important for pine infection were typically the only spore stage found; whereas, one *Ribes* species (*R. ineme*) was predominantly producing alternate host-infecting urediniospores. Having urediniospores and teliospores predominating on different hosts may have the potential to broaden the period within the growing season when whitebark pine infection is possible.

Finally, if non-*Ribes* alternate hosts are significant sources of pine infection, then management that creates openings for pine regeneration may need to account for complex interactions with these alternate hosts. Research studies aimed at understanding the dynamic interactions of *C. ribicola* with its non-*Ribes* alternate hosts are therefore necessary to develop effective management and restoration for whitebark pine.

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Figure 1. The underside of a leaf of *Pedicularis racemosa* showing an infection caused by the white pine blister rust fungus, *Cronartium ribicola*. The hair-like structures are columns of teliospores, and are the most prevalent sign of infection on non-*Ribes* alternate hosts. (Photo: J. Hanna).■